# SOFT SEDIMENT BENTHIC MACROINVERTEBRATE COMMUNITIES OF THE GREEN RIVER AT THE OURAY NATIONAL WILDLIFE REFUGE, UINTAH COUNTY, UTAH

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ABSTRACT.—Benthic macroinvertebrates from four habitat types (river channel, ephemeral side channel, river backwater, and seasonally inundated wetland) were examined from the Green River at the Ouray National Wildlife Refuge, Uintah County, UT, June–August 1991. Four major taxa (Nematoda, Oligochaeta, Diptera: Ceratopogonidae, and Chironomidae) were quantified. Cluster analysis of densities showed that habitat types with comparable flow conditions were the most similar. Highest to lowest overall benthic invertebrate densities of the four habitats were as follows: ephemeral side channel, river backwater, seasonally inundated wetland, and river channel. Nematodes were the most abundant taxon in all habitat types and sample dates except the August sample of the river channel and river backwater and the July sample of the seasonally inundated wetland.

Key words: benthic macroinvertebrates, Nematoda, Oligochaeta, Ceratopogonidae, Chironomidae, river benthos, wetland, benthos, Green River.

In 1962 Flaming Gorge Dam was completed on the Green River in northeastern Utah. This, in addition to dikes constructed along the river's course and the introduction of nonnative fishes. has altered natural conditions such that many native fishes have reached the brink of extinction and are now listed as endangered species. Grabowski and Hiebert (1989) studied the Green River below Flaming Gorge Dam and noted the importance of backwaters as nursery habitats to introduced and native fishes. They found the most important food items to be benthic macroinvertebrates, predominantly chironomid larvae. Their investigation was confined to two habitats: the main channel and river backwaters. We also studied benthic communities of the river channel and backwater habitats and two additional habitats-seasonally inundated wetlands and ephemeral side channels. No published information exists about the community structure of benthic macroinvertebrates in these latter two habitat types.

Benthic invertebrates of large rivers are poorly known. Difficulty in sampling, the amount of time needed to process samples, identification of specimens after collection, and heterogeneity of habitats make study difficult and often expensive. Studies of riverine systems have utilized divergent methodologies. Some studies randomly sample an entire river cross section and do not attempt to quantify different river habitat types (Grzybkowska 1989, Grzybkowska et al. 1990, Munn and Brusven 1991). Other studies have been directed toward specific river habitats such as riffles (Rader and Ward 1988, Morgan et al. 1991), floodplains (Gladden and Smock 1990), or tailwaters of reservoirs (Swink and Novotny 1985). Relatively few have simultaneously studied multiple habitat types in a single river system (Beckett et al. 1983, Grabowski and Hiebert 1989).

Our purpose was to determine densities and community assemblages of the major benthic macroinvertebrates in four Green River habitats: river channel, ephemeral side channel, river backwater, and seasonally inundated wetland. Benthic samples were taken from June through August 1991, in the Green River at the Ouray National Wildlife Refuge, Uintah County, UT, USA.

#### STUDY SITES

The Green River originates in Wyoming and flows south through eastern Utah to its confluence with the Colorado River (Fig. 1). It adds more volume to the Colorado River system than any other tributary. In eastern Utah, at river km 404, the Green River enters the Ouray National

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Wildlife Refuge. This section of the river has the lowest gradient of the entire Green River system. Riparian vegetation consists of willow and tamarix with occasional cottonwoods. We collected monthly samples in the Ouray National Wildlife Refuge (see also Fig. 2). In addition to benthic samples, water chemistry was determined for each habitat type on each sample date (Table 1). Salinity and conductivity were recorded with a YSI meter (Yellowstone Instruments); turbidity was measured with a nephelometer; and hardness, pH, and alkalinity were determined with a Hach Kit (Hach Chemical Corporation). Water chemistry was recorded at three locations per sample area on each sample date. At each site, a min-max thermometer was placed near the benthos-water interface at the time of sampling and left for 10 days. Substrate composition was estimated visually.

## **River Channel**

The river channel was sampled approximately 1.3 km north of the United States Fish and Wildlife Service (USFWS) hatchery on the Ouray National Wildlife Refuge. Sampling was adjacent to a sand bar that decreased water turbulence and prevented shifting sands. Water chemistry values were relatively stable. Turbidity was substantially higher during the August sample. Substrate consisted mostly of sand with

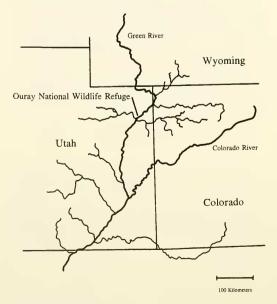


Fig. 1. Regional map showing the location of the Ouray National Wildlife Refuge.

little silt and detritus. Water levels were too high during June (peak flow) to allow sampling.

# Ephemeral Side Channel

During high flows the Green River will occupy various smaller channels that are dry during low-flow intervals. We have named such habitats "ephemeral side channels." The ephemeral side channel studied was approximately 2.75 km south of the USFWS hatchery. For most of the year water levels in the main channel were below the level of the ephemeral side channel. However, during peak flow, water filtered through a wooded area and gathered into the channel, which was 10 m wide and 500 m long. As the river level dropped, flow slowed and eventually stopped. Because the side channel dried up shortly after the July sample, no August sample was taken. Most notable of the water chemistry measurements was the increase of salinity and alkalinity when comparing June to July. Water temperature also deviated more during July. Substrate consisted mostly of firm silt and detritus with little sand. Sediment deposition contributed little to the site during our study.

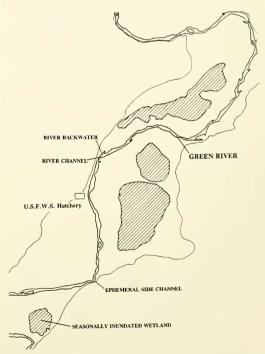


Fig. 2. Local map of the Ouray National Wildlife Refuge, Uintah County, UT, showing the location of sampling sites.

TABLE 1. Mean  $\pm$  standard deviation water chemistry values from Green River sample sites, June–August 1991 (n = 3, temperature in °C, salinity in percent, conductivity in  $\mu$ mhos, turbidity in NTUs, hardness and alkalinity in ppm CaCO<sub>3</sub>).

| Habitat type    | Date       | Min./max<br>temp. | pН             | Salinity      | Conductivity  | Turbidity     | Hardness     | Alkalinity    |
|-----------------|------------|-------------------|----------------|---------------|---------------|---------------|--------------|---------------|
| River channel   |            |                   |                |               |               |               |              |               |
|                 | 7/15       | *                 | $8.14 \pm .09$ | $.04 \pm .0$  | $753 \pm 6$   | $183 \pm 318$ | $411 \pm 0$  | $-183 \pm 10$ |
|                 | 8/12       | 20.5/26.5         | $8.48 \pm .10$ | $.04 \pm .01$ | $718 \pm 8$   | $402 \pm 41$  | $320 \pm 20$ | $205 \pm 17$  |
| Ephemeral side  | e channel  |                   |                |               |               |               |              |               |
| *               | 6/3        | 20.5/30.5         | $9.0 \pm 0$    | $.03 \pm .06$ | $326 \pm 10$  | $57 \pm 6$    | $183 \pm 20$ | $171 \pm 0$   |
|                 | 7/1        | 16/30.5           | $9.14 \pm .16$ | $.12 \pm .03$ | $445 \pm 5$   | $127 \pm 21$  | $228 \pm 10$ | $240 \pm 17$  |
| River backwate  | r          |                   |                |               |               |               |              |               |
|                 | 7/10       | 20.5/29.5         | $7.98 \pm .23$ | $.01 \pm .01$ | $523 \pm 23$  | $57 \pm 9$    | $228 \pm 10$ | $183 \pm 20$  |
|                 | 8/8        | 19/26.5           | $8.59 \pm .12$ | $.03 \pm .0$  | $730 \pm 111$ | $45 \pm 11$   | $268 \pm 40$ | $228 \pm 26$  |
| Seasonally inur | dated wetl | and               |                |               |               |               |              |               |
|                 | 6/10       | 19.5/26.5         | $9.0 \pm 0$    | $.02 \pm .0$  | $314 \pm 8$   | $52 \pm 8$    | $154 \pm 0$  | $143 \pm 10$  |
|                 | 7/12       | 22/32             | $8.37 \pm .11$ | $.02 \pm .01$ | $446 \pm 20$  | $36 \pm 8$    | $205 \pm 0$  | $223 \pm 0$   |
|                 | 8/15       | 22/29.5           | $8.93\pm.1$    | $.01 \pm .0$  | $345 \pm 13$  | $195\pm17$    | $171\pm17$   | $154\pm0$     |

\*Thermometer lost

# River Backwater

River backwaters are submerged during high flows and do not emerge as distinct entities until the river drops. For this reason the river backwater was not sampled during peak flow (June). The river backwater we sampled, located just upstream of the river channel site described above, was approximately 10 m wide  $\times$  50 m long and 1.3 m deep. Turbidity, alkalinity, and pH were highest during the August sample. Substrate consisted mostly of loose silt and detritus with virtually no sand. Silt and detritus were constantly being deposited during the study period.

## Seasonally Inundated Wetland

This site, commonly called "Old Charlie's Wash," is a shallow floodplain wetland managed by the USFWS for waterfowl and is located approximately 4.3 km south of the USFWS hatchery. As the river rises in the spring, water enters Old Charlie's Wash and, at peak flow, retaining structures are put in place to create a 43-ha pond and to prevent the impounded water from receding as rapidly as the river. By early fall the water in Old Charlie's Wash is nearly depleted by seepage and evaporation. Turbidity increased dramatically during the August sample, and conductivity, hardness, and alkalinity peaked during the July sample. Substrate consisted of firm silt, detritus, and sand.

## METHODS

# Sampling

Samples were collected during the summer of 1991 (Tables 2-5). Initial sampling of the ephemeral side channel and seasonally inundated wetland occurred just after river flow peaked in early June, but samples for the river channel and backwater habitats were not collected because the water level was too high. All four habitats were sampled during July and all but the ephemeral side channel during August. Fifty core samples were taken along a 30-m transect at each site. Each sample was collected with a clear acrylic tube, 450 mm long imes47 mm in diameter (Shiozawa 1985), which was pushed into the substrate to a depth of 60-80 mm. Sediment from each sample was preserved in 5% formalin with rose bengal stain added to aid in sample sorting.

## Sample Processing

In the laboratory we washed each sample to separate organisms from sediments using the following procedure. First, the formalin was drained and replaced with tap water. The sample was then gently stirred to resuspend the sediments and poured into a plastic tray (36.5 cm  $\times$  31.5 cm  $\times$  6 cm) through which a small volume of warm water flowed. The outflowing water, laden with small sand and clay particles, detritus, and benthic invertebrates, was filtered through a 63-µm screen. Larger

|                 | 15 July 199                       | 1                      | 12 August 1991                    |                           |  |  |
|-----------------|-----------------------------------|------------------------|-----------------------------------|---------------------------|--|--|
| Taxon           | Density/m <sup>2</sup> (95% C.L.) | # of samples processed | Density/m <sup>2</sup> (95% C.L.) | # of samples<br>processed |  |  |
| Nematoda        | 24,881 (13,107-47,302)            | 6                      | 2421 (2063-2840)                  | 5                         |  |  |
| Oligochaeta     | 3426 (2565-4570)                  | 18                     | 11,182 (7497-16,678)              | 5                         |  |  |
| Insecta         |                                   |                        |                                   |                           |  |  |
| Ceratopogonidae | 3608 (2731-4767)                  | 27                     | 13,026 (9316-18,215)              | 5                         |  |  |
| Chironomidae    | 4150 (2798–6155)                  | 5                      | 3516 (2454-5037)                  | 30                        |  |  |
| Early instars   | 1037                              |                        | 3016                              |                           |  |  |
| Chironomus      | 346                               |                        | 0                                 |                           |  |  |
| Cyphomella      | 0                                 |                        | 58                                |                           |  |  |
| Lenziella       | 576                               |                        | 0                                 |                           |  |  |
| Paramerina      | 115                               |                        | 0                                 |                           |  |  |
| Paratendipes    | 0                                 |                        | 96                                |                           |  |  |
| Polypedilum     | 1844                              |                        | 269                               |                           |  |  |
| Procladius      | 115                               |                        | 0                                 |                           |  |  |
| Psectrocladius  | 115                               |                        | 0                                 |                           |  |  |
| Stempellinella  | 0                                 |                        | 58                                |                           |  |  |
| Tanytarsus      | 0                                 |                        | 19                                |                           |  |  |

TABLE 2. Densities of benthic invertebrates  $(\#/m^2)$  from the Green River, river channel habitat, Ouray National Wildlife Refuge, Ouray, UT.

TABLE 3. Densities of benthic invertebrates (#/m<sup>2</sup>) from the Green River, ephemeral side channel habitat, Ouray National Wildlife Refuge, Ouray, UT.

|                  | 3 June 1991                       |                           | 1 July 1991                       |                           |  |  |
|------------------|-----------------------------------|---------------------------|-----------------------------------|---------------------------|--|--|
| Taxon            | Density/m <sup>2</sup> (95% C.L.) | # of samples<br>processed | Density/m <sup>2</sup> (95% C.L.) | # of samples<br>processed |  |  |
| Nematoda         | 261,680 (88,934-769,968)          | 5                         | 302,603 (215,886-424,154)         | 5                         |  |  |
| Oligochaeta      | 2728 (2096-3546)                  | 15                        | 12,796 (10,681-15,329)            | 5                         |  |  |
| Insecta          |                                   |                           |                                   |                           |  |  |
| Ceratopogonidae  | 0                                 | 30                        | 0                                 | 5                         |  |  |
| Chironomidae     | 2325 (1843-2927)                  | 30                        | 8185 (6385-10,491)                | 5                         |  |  |
| Early instars    | 979                               |                           | 2075                              |                           |  |  |
| Chironomus       | 1134                              |                           | 3112                              |                           |  |  |
| Cryptochironomus | 0                                 |                           | 115                               |                           |  |  |
| Cryptotendipes   | 19                                |                           | 461                               |                           |  |  |
| Lenziella        | 96                                |                           | 1383                              |                           |  |  |
| Polypedilum      | 19                                |                           | 692                               |                           |  |  |
| Procladius       | 0                                 |                           | 346                               |                           |  |  |
| Tanypus          | 19                                |                           | 0                                 |                           |  |  |
| Tanytarsus       | 58                                |                           | 0                                 |                           |  |  |

sediment particles (sands and structural clays) that remained in the plastic tray were periodically examined for specimens. If none were found, the sediments were discarded. Material collected on the screen was stored in 70% ETOH.

Samples sorted were randomly chosen from the 50 samples taken at each site and date. Each sample was placed in glass petri dishes (from one to six dishes depending on the amount of material) and sorted under a dissecting microscope (see Tables 1–4 for number of samples processed). Four major taxa (Nematoda, Oligochaeta, Ceratopogonidae, and Chironomidae) were counted. Only Chironomidae were identified to the generic level. Miscellaneous taxa were also recorded but were not quantified (see Table 5).

The number of samples sorted from each site and sampling date was determined as follows: 5 of the 50 samples were randomly selected and the four major taxa were counted. Because of their contagious distribution (determined by calculating variance to mean ratios), numbers of individuals of each taxon were then log transformed (x + 1). The variance and mean

| <b>2</b> | 1 | 7 |
|----------|---|---|
|          |   |   |

|                 | 10 July 1991                      | L                      | 8 August 1991                     |                           |  |  |
|-----------------|-----------------------------------|------------------------|-----------------------------------|---------------------------|--|--|
| Taxon           | Density/m <sup>2</sup> (95% C.L.) | # of samples processed | Density/m <sup>2</sup> (95% C.L.) | # of samples<br>processed |  |  |
| Nematoda        | 54,872 (24,350-123,650)           | 5                      | 134,183 (94,656–190,542)          | 5                         |  |  |
| Oligochaeta     | 26,642 (14,622-48,495)            | 9                      | 164,731 (101,881-266,728)         | 5                         |  |  |
| Insecta         |                                   |                        |                                   |                           |  |  |
| Ceratopogonidae | 96 (90-107)                       | 30                     | 461 (385-552)                     | 30                        |  |  |
| Chironomidae    | 31,125 (15,356-63,089)            | 5                      | 22,863 (12,139-43,136)            | 6                         |  |  |
| Early instars   | 8877                              |                        | 7301                              |                           |  |  |
| Chironomus      | 7032                              |                        | 6340                              |                           |  |  |
| Lenziella       | 346                               |                        | 1249                              |                           |  |  |
| Polypedilum     | 14,179                            |                        | 5860                              |                           |  |  |
| Procladius      | -461                              |                        | 1345                              |                           |  |  |
| Psectrocladius  | 115                               |                        | 0                                 |                           |  |  |
| Tanytarsus      | 115                               |                        | 769                               |                           |  |  |

TABLE 4. Densities of benthic invertebrates  $(\#/m^2)$  from the Green River, river backwater habitat, Ouray National Wildlife Refuge, Ouray, UT.

TABLE 5. Densities of benthic invertebrates  $(\#/m^2)$  from the Green River, seasonally inundated wetland habitat, Ouray National Wildlife Refuge, Ouray, UT.

|                 | 10 June 1991                         |                        | 12 Jul                               | y 1991                   | 15 August                              | 15 August 1991            |  |  |
|-----------------|--------------------------------------|------------------------|--------------------------------------|--------------------------|--|---------------------------|--|--|
| Taxon           | Density/m <sup>2</sup><br>(95% C.L.) | # of samples processed | Density/m <sup>2</sup><br>(95% C.L.) | # of sample<br>processed | s Density/m <sup>2</sup><br>(95% C.L.) | # of samples<br>processed |  |  |
| Nematoda        | 7133 (4534-11,266)                   | 8                      | 80,694 (38,595-168,                  | 713) 5                   | 88,533 (83,125-94,784                  | ) 5                       |  |  |
| Oligochaeta     | $4573\ (3402{-}6141)$                | 30                     | 87,150 (39,242-193,3                 | 547) 10                  | 22,249 (11,930-41,494                  | ) 5                       |  |  |
| Insecta         |                                      |                        |                                      |                          |  |                           |  |  |
| Ceratopogonidae | 0                                    | 30                     | 0                                    | 14                       | 2478 (1941–3165)                       | 20                        |  |  |
| Chironomidae    | 903 (895-915)                        | 30                     | 23,055 (13,707-38,7                  | 80) 14                   | 3977 (2816-5617)                       | 10                        |  |  |
| Early instars   | 96                                   |                        | 8769                                 |                          | 2479                                   |                           |  |  |
| Ablabesmyja     | 0                                    |                        | 124                                  |                          | 0                                      |                           |  |  |
| Chironomus      | 154                                  |                        | 41                                   |                          | 576                                    |                           |  |  |
| Cricotopus      | 19                                   |                        | 453                                  |                          | 0                                      |                           |  |  |
| Cryptochironom  | nus 134                              |                        | 206                                  |                          | 0                                      |                           |  |  |
| Cryptotendipes  | 58                                   |                        | 947                                  |                          | 346                                    |                           |  |  |
| Glyptotendipes  | 58                                   |                        | 988                                  |                          | 0                                      |                           |  |  |
| Lenziella       | 115                                  |                        | 1112                                 |                          | 0                                      |                           |  |  |
| Microtendipes   | 0                                    |                        | 1029                                 |                          | 0                                      |                           |  |  |
| Paratanytarsus  | 231                                  |                        | 6505                                 |                          | 58                                     |                           |  |  |
| Polypedilum     | 19                                   |                        | 2388                                 |                          | 173                                    |                           |  |  |
| Procladius      | 0                                    |                        | 124                                  |                          | 58                                     |                           |  |  |
| Psectrocladius  | 0                                    |                        | 41                                   |                          | 0                                      |                           |  |  |
| Tanypus         | 0                                    |                        | 124                                  |                          | 173                                    |                           |  |  |
| Tanytarsus      | 0                                    |                        | 206                                  |                          | 115                                    |                           |  |  |
| Zavrelia        | 19                                   |                        | 0                                    |                          | 0                                      |                           |  |  |

were used in the following formula to estimate the number of samples to process (Elliot 1977):

$$N = \frac{S^2}{d^2 \overline{x}^2}$$

where N = number of samples to process, S = variance, d = level of accuracy desired for the

sample (in this case 0.1), and  $\overline{x}$  = the mean. For our samples d was chosen to be 0.1, for an accuracy within 10% of the mean. If, after five samples were processed, N was <5 for a specific taxonomic group, no more samples were processed for that group. Those taxa for which N was >5 were counted in an additional sample. The mean and variance for taxa not eliminated were again calculated using the additional sample value(s) and above formula. This process continued until *N* was less than the number of samples already processed for the taxon. Because of time and financial constraints, we never picked more than 30 samples for any specific habitat and sample date. All sorted samples were preserved in 70% ETOH.

Chironomids were removed from 70% ETOH and placed in distilled water for 10–15 min prior to clearing. Individual specimens were placed in hot ( $\approx$ 80°C) 10% KOH (Cranston 1982) for 5–15 min to clear (larger specimens required more time to clear). After clearing, specimens were transferred to distilled water for at least 5 min. Each specimen was then placed in glycerine on a microscope slide for identification. Only late instars were identifiable. Representative specimens of each genus encountered were permanently mounted. Specimens were classified to the generic level using keys by Mason (1968), Wiederholm (1983), and Merritt and Cummins (1984).

# Data Analysis

Average densities  $(\#/m^2)$  and 95% confidence limits for each of the four main taxa and each genus of Chironomidae were calculated for each sample site and date. Because density distributions were contagious, 95% confidence intervals were calculated for each of the four main taxa using a logarithmic transformation suggested by Elliot (1977; Tables 2–5). These

values were then applied to the arithmetic mean (Shiozawa and Barnes 1977). Confidence intervals were not calculated for each genus in the Chironomidae because densities of some genera were too low.

Cluster analysis was performed using the statistical package NTSYS-pc (Rohlf 1992). Several dissimilarity measures, including Bray-Curtis, Canberra's, and Renkonen's, were used to generate distance matrices. A comparison of each of these matrices to the original data showed that the Bray-Curtis measure (Bray and Curtis 1957) provided the best "fit" of the eluster analysis to the data. Average linkage clustering of the Bray-Curtis distances, based on the mean number of individuals/m<sup>2</sup> of each species between habitat types and sample dates, was done with the unweighted pair-group method using arithmetic averages (UPGMA; Krebs 1989).

#### RESULTS

## Invertebrates

Nematodes occurred in every sample processed and were most abundant in the July sample of the ephemeral side channel habitat (302,603/m<sup>2</sup>) and least abundant in the river channel August sample (2421/m<sup>2</sup>; Tables 2–5). They comprised the majority of benthic invertebrates in all habitats and sample dates except

TABLE 6. Functional group (Merritt and Cummins 1984) and habitat association of Chironomidae genera from the Green River, Ouray National Wildlife Refuge, Ouray, UT.

|                    |            | Functior  |           |         |                      |  |
|--------------------|------------|-----------|-----------|---------|----------------------|--|
| Taxon              | Collectors | Predators | Shredders | Unknown | Habitat association' |  |
| Ablabesmyja        |            | X         |           |         | SIW                  |  |
| Chironomus         | X          |           |           |         | RC,ESC,RB,SIW        |  |
| Cladotanytarsus    |            |           |           | Х       | RC,ESC,RB,SIW        |  |
| Cricotopus         | X          |           | Х         |         | SIW                  |  |
| Cryptochironomus   |            | X         |           |         | ESC,SIW              |  |
| Cryptotendipes     |            |           |           | Х       | ESC,SIW              |  |
| nr. Cyphomella     | Х          |           |           |         | RC                   |  |
| Glyptotendipes     | X          |           | X         |         | SIW                  |  |
| Microtendipes      | X          |           |           |         | SIW                  |  |
| Paramerina         |            |           |           | Х       | RC                   |  |
| Paratanytarsus     |            |           |           | Х       | SIW                  |  |
| Paratendipes       | Х          |           |           |         | RC                   |  |
| Polypedilum        | Х          | Х         | Х         |         | RC,ESC,RB,SIW        |  |
| Procladius         | Х          | Х         |           |         | RC,ESC,RB,SIW        |  |
| Psectrocladius     | Х          |           | Х         |         | RC,RB,SIW            |  |
| nr. Stempellinella |            |           |           | Х       | RC                   |  |
| Tanypus            | Х          | X         |           |         | ESC,SIW              |  |
| Tanytarsus         | Х          |           |           |         | RC,ESC,RB,SIW        |  |
| Zavrelia           | Х          |           |           |         | SIW                  |  |

\*RC = river channel, ESC = ephemeral side channel, RB = river backwater, SIW = seasonally inundated wetland.

the August river channel and river backwater habitats and the July wetland sample.

Oligochaetes were present in all habitat types and on all sample dates. Densities ranged from a low of  $2728/m^2$  in the June ephemeral side channel sample to a high of  $164,731/m^2$  in the July river backwater sample (Tables 2–5).

The lowest abundance of Ceratopogonids was observed in the July river backwater sample (96/m<sup>2</sup>). Their density was 136X greater in the river channel August sample (13,026/m<sup>2</sup>; Tables 2–5). Ceratopogonids were absent from both June and July samples of the seasonally inundated wetland and the ephemeral side channel.

Ninteen chironomid genera were collected during this study. Fourteen genera were found in the July seasonally inundated wetland samples, and five genera occurred in the August river channel and river backwater samples. Seven genera occurred in only one habitat or on only one date. Six genera were found in the seasonally inundated wetland habitat only, and four occurred only in the river channel. No chironomid genus was unique to the ephemeral side channel or the river backwater. The genus *Polypedilum* was collected in all habitat types and on all sample dates. Total chironomid densities were least (903/m<sup>2</sup>) in the June sample of the seasonally inundated wetland and greatest (31,125/m<sup>2</sup>) in the July river backwater sample (Tables 2–5). Unidentifiable early instars were collected in all habitat types and in all sample periods and comprised 86% of the river channel sample in August. The most common functional group category of the Green River chironomids was collectors followed by predators and shredders. Specific functional group and Green River habitat association for each genus are presented in Table 6.

Other insects found in the samples are listed in Table 7. Density estimates would not be valid for these taxa because of their ability to avoid the core sampler.

## **Cluster Analysis**

The UPGMA cluster analysis of the benthic invertebrate communities in each habitat type and sample date indicated that sites with similar flow conditions tended to cluster together (Fig. 3). A matrix comparison of original distances calculated using the Bray-Curtis coefficient with distances implied from the dendrogram is presented in Figure 4. Correlation between the two was high (R = .907), implying that the dendrogram is an accurate representation of

|                              |      | River Ephemeral<br>channel side channel |      | · · · · · · · · · · · · · · · · · · · |      |        |      |      |        |  | nally inundated<br>wetland |  |
|------------------------------|------|---|------|---------------------------------------|------|--------|------|------|--------|--|----------------------------|--|
| Taxon                        | July | August                                  | June | July                                  | July | August | June | July | August |  |                            |  |
| Coleoptera                   |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Hydrophilidae (larvae)       |      |   |      |                                       |      |        | Х    |      |        |  |                            |  |
| Diptera                      |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Chironomidae (pupae)         |      | Х                                       |      |                                       | Х    | Х      | Х    | Х    |        |  |                            |  |
| Empididae (larvae)           |      |   |      | Х                                     |      | X      |      |      |        |  |                            |  |
| Simuliidae (larvae)          |      | Х                                       |      |                                       |      |        |      |      |        |  |                            |  |
| Ephemeroptera                |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Baetidae                     |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Baetis (nymph)               |      | Х                                       |      |                                       | Х    | Х      |      | Х    | Х      |  |                            |  |
| Callibaetis (nymph)          |      |   |      |                                       | Х    |        |      |      |        |  |                            |  |
| Caenidae                     |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Caenis (nymph)               |      |   |      | Х                                     | Х    |        |      | Х    |        |  |                            |  |
| Tricorythidae                |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| <i>Tricorythodes</i> (nymph) | Х    |   |      |                                       |      |        |      |      |        |  |                            |  |
| Hemiptera                    |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Corixidae                    |      | Х                                       |      |                                       | Х    | Х      |      |      |        |  |                            |  |
| Odonata                      |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Coenagrionidae               |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Ischnura (nymph)             |      |   |      |                                       |      |        |      | Х    | Х      |  |                            |  |
| Gomphidae (nymph)            |      | X                                       |      |                                       |      |        |      |      |        |  |                            |  |
| Plecoptera                   |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Perlodidae (nymph)           |      |   |      |                                       |      |        |      |      |        |  |                            |  |
| Isoperla                     | X    |   |      |                                       |      |        |      |      |        |  |                            |  |

TABLE 7. Other insects encountered in the Green River ecosystem, June-August 1991.

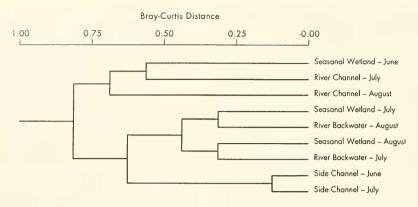


Fig. 3. UPGMA cluster analysis of Green River habitat types located in the Ouray National Wildlife Refuge.

the original Bray-Curtis distances. Ephemeral side channel samples show the greatest similarity (least distance), and wetland and backwater sites are more similar to one another.

## DISCUSSION

## Nematoda

The importance of free-living nematodes in aquatic systems has not been extensively studied. Aquatic nematodes are known to be microbotrophic, predaceous, and/or parasitic during one or more of their life stages (Poinar 1991). Due to the scarcity of adequate keys and their small size, nematodes are seldom listed beyond the phylum designation in most studies and may not even be quantified. In studies of aquatic systems where nematodes are quantified, highest densities have been found in lakes. Strayer (1985) and Nalepa and Quigley (1983) reported that nematodes comprised 60% and 80%, respectively, of all benthic metazoans in Mirror Lake, NH, and in Lake Michigan with means of 680,000/m<sup>2</sup> (Mirror Lake) and 260,000/ m<sup>2</sup> (Lake Michigan). In contrast, Palmer (1990) in Goose Creek and Gladden and Smoek (1990) on the floodplain of Colliers Creek reported that nematodes comprised a much smaller percentage (6% of total invertebrates) and occurred at diminished densities (1000-15,000/  $m^2$  and 1746/ $m^2$ , respectively) in lotic systems.

In our study nematode density estimates from the seasonally inundated wetland June sample (7133/m<sup>2</sup>) and the July and August river channel samples (24,881/m<sup>2</sup> and 2421/m<sup>2</sup>, respectively) are comparable to densities previously reported from lotic systems (Gladden and Smock 1990, Palmer 1990). Density esti-

mates for all other sites and dates (54.872– 302,603/m<sup>2</sup>) are more similar to densities in lentic habitats (see above). Greater densities are achieved in the more stable benthic environments provided by calmer waters and finer sediment particle size. In their study of White Clay Creek, Bott and Kaplan (1989) found that nematode densities were greater in silt than in sand. In our study the highest densities are also associated with a low sand content in the substratum. Low densities reported for the June sample of the seasonally inundated wetland site reflect the relatively short time that water had been on the sample site. Of the four major invertebrate groups collected in this study, nematodes accounted for 8% of the individuals in the river channel August sample and 98% in the June ephemeral side channel. Nematodes accounted for 67.7% of all organisms observed. Palmer (1990), using a 3.3-cm-dia. core and 44- $\mu$ m mesh, reported that nematodes constituted only 4-15% of the Goose Creek community, with a mean of 9%. Her data are similar to our river channel values. High nematode densities and their high percentage of the total invertebrates that we report from the ephemeral side channel, river backwater, and seasonally inundated wetland are unusual and should be compared to samples taken at similar locations in this and other large rivers using comparable methods.

### Oligochaeta

Freshwater oligochaetes are a well-studied and diverse group found in every type of estuarine and freshwater habitat. They feed mostly on bacteria living in soft sediments (Brinkhurst and Gelder 1991). The amount and quality of



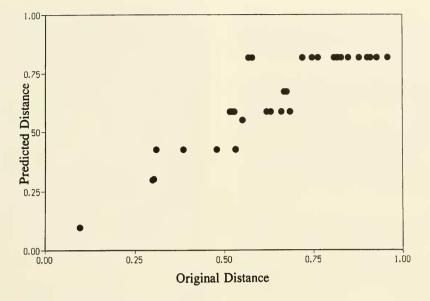


Fig. 4. Comparison of original dissimilarity matrix and implied matrix from the dendrogram.

organic matter found in the sediment are primary factors determining which species will be present in a particular area (Brinkhurst and Cook 1974). We identified our specimens only to class level. Oligochaete densities in nonpolluted lakes are lower than those in organically polluted waters. Densities in Mirror Lake ranged from 30,000 to 33,000/m<sup>2</sup> (Strayer 1985). Ionasson and Thorhauge (1976) reported oligochaete densities in Lake Esrom, Denmark, of 6000-12,000/m<sup>2</sup>. Brinkhurst and Cook (1974) found that densities of the three most common tubificids in the more polluted areas of Toronto Harbor ranged from 51,000 to 197,000/m<sup>2</sup>. Oligochaete densities in nonpolluted lotic systems tend to be lower. Grzybkowska and Witczak (1990) report oligochaete densities in the lower Grabia River, Poland, ranging from 110 to 900/m<sup>2</sup>, and Palmer (1990) reports densities from 5000 to 15,000/m<sup>2</sup> in Goose Creek, VA. Densities from polluted lotic systems can approach  $200,000/\text{m}^2$  (Koehn and Frank 1980).

Oligochaete densities in the seasonally inundated wetland June sample  $(87,150/m^2)$  and river backwater August sample  $(164,731/m^2)$ are comparable to values observed in polluted systems described above. Densities from both ephemeral side channel samples  $(2728 m^2 and$  $12,796/m^2)$  and both river channel samples  $(3426/m^2 and 11,182/m^2)$  are comparable to those in Goose Creek (Palmer 1990). In general, oligochaete densities in our study were higher in habitats with the least amount of water flow (seasonally inundated wetland and river backwater habitat types). Terrestrial vegetation invades wetlands during dry periods, and when the water returns the following spring, decaying vegetation forms a rich food base. Backwater habitats retain fine particles, including detritus, being transported by the river; as summer progresses, this creates an enriched food base. These factors are the likely reason for the convergence oligochaete densities in these two habitats with those in organically polluted systems.

## Ceratopogonidae

The study of ceratopogonids has mainly centered on adults because of their economic importance (Davies and Walker 1974). Larvae inhabit a variety of habitats including tree holes, leafpacks, and pitcher plants, but are usually most numerous in shallow areas of streams, lakes, and ponds (Bowen 1983). Aquatic forms are mostly predaceous (Merritt and Cummins 1984), but several species are known to consume algae and plant debris (Kwan and Morrison 1974).

Corkum (1990) investigated streams associated with different land-use types in southwestern Ontario and found densities of 50/m<sup>2</sup> in "forested" sites, 480/m<sup>2</sup> in "mixed" sites, and 5300/m<sup>2</sup> in "farmland" sites. Adamek and Sukop (1992) found maximum densities of only  $1/m^2$  on over-flooded meadows in Czechoslovakia. In Lake Norman, NC, Bowen (1983) reported a mean larval ceratopogonid density of 767/m<sup>2</sup>.

Ceratopogonid densities reached a peak in the August river channel sample (13,026/m<sup>2</sup>)much higher than any reported in the literature above. In their study of the Green River, Grabowski and Hiebert (1989) did not report densities, but did conclude that ceratopogonids were more abundant in river channel samples than in backwaters. Our study supports this conclusion. Average densities for the river channel July and August samples were 3608/m<sup>2</sup> and  $13,026/m^2$ , respectively, compared to  $96/m^2$ and 461/m<sup>2</sup> for the backwater July and August samples. Ceratopogonid larvae were completely absent from the ephemeral side channel as well as the June and July seasonally inundated wetland samples.

### Chironomidae

Chironomidae are typically the most abundant macroinvertebrates in lentic (Strayer 1985) and lotic (Grzybkowska and Witczak 1990) systems. Studies of relatively small geographical areas have reported impressive numbers of species. For instance, Douglas and Murray (1980) found 142 species in Killarney Valley, Ireland. High diversity of chironomids makes them important as indicators of environmental condition (Wingard and Olive 1989). They are also abundant and provide an important food source for fish (Brown et al. 1980, Winkel and Davids 1987, Grabowski and Hiebert 1989), waterfowł (Titmus and Baddock 1980), and other migratory birds (Bowman 1980).

We identified 19 chironomid genera from our sites within the Green River ecosystem. Other investigations of lotic systems have yielded similar numbers—12 genera in the upper Tusearawas River, OH (Wingard and Olive 1989), 24 genera in the River Frome, England (Pinder 1980), 25 genera in the Mississippi River (Beekett et al. 1983), and 36 genera in Juday Creek, IN (Berg and Hellenthal 1991). Grabowski and Hiebert (1989) studied the Green River in the same general area considered in our study and also identified 19 genera. However, only seven of the genera reported by the latter authors were found in our study: Chironomus, Cricotopus, Cryptochironomus, Polypedilum, Procladius, Tanypus, and Tanytarsus.

Densities of chironomids in aquatic systems can vary substantially. In a study of Lake Vissavesi, Finland, Paasivirta and Koskenniemi (1980) reported densities of  $64/m^2$  in a coarse debris habitat and 2997/m<sup>2</sup> in a moss-grown site. Jonasson and Lindegaard (1979) reported 59,000/m<sup>2</sup> from Lake Myvath, Iceland, Variability in lotic systems has also been documented. Pinder (1980) reported densities from a low of 48/m<sup>2</sup> to 6273/m<sup>2</sup> in a chalk stream in England, and Grzybkowska (1989) found 10,664/m<sup>2</sup> in the River Grabia, Poland. While no distinct trends exist when comparing chironomid densities in lentic and lotic systems, densities are influenced by sediment size (Paasivirta and Koskenniemi 1980, Beckett et al. 1983).

Chironomid densities from the July and August river channel samples were 4148/m<sup>2</sup> and 3516/m<sup>2</sup>, respectively. River backwater samples were  $31,125/m^2$  and  $22,864/m^2$  for the same times. Grabowski and Hiebert (1989) reported maximum chironomid densities in the same area of the Green River of less than 100/m<sup>2</sup> for the river channel and 2800/m<sup>2</sup> for river backwaters—substantially less than our estimates. It is possible that annual differences in seasonal discharge, area of the sampling device, and later sampling period all contributed to this discrepancy. However, because of significant differences in mesh size  $(63-\mu m)$ ours, 600-µm Grabowski and Hiebert's), data of Grabowski and Hiebert and ours cannot be considered equivalent. It is worth noting that mesh sizes larger than  $100 \,\mu$ m have been shown to negatively bias density estimates (Straver 1985).

## Community Similarity

Cluster analysis of the data showed that, in general, habitat types clustered together independent of sample date, suggesting that the different habitat types studied in the Green River are distinct. Beckett et al. (1983), for example, studied five habitats in the Mississippi River and also found them to remain compositionally distinct regardless of flow and sample date. Distribution and abundance of benthic macroinvertebrates characteristic of these habitat types have been attributed to flow conditions and sediment size in our study. Since flow conditions are the major determinant of particle size, flow conditions are likely the determining factor. This conclusion has also been reached by other investigators (Beckett et al. 1983, Statzner and Higler 1986).

Grabowski and Hiebert (1989) concluded that benthic macroinvertebrate densities in backwaters of the Green River were higher than those of the river channel. Our data suggest that the seasonally inundated wetland and ephemeral side channel are also valuable habitats and have the potential to contribute substantial biomass to the Green River system. Oligochaete and chironomid densities reported in our study are comparable to other lotic systems (Koehn and Frank 1980, Pinder 1980, Grzybkowska 1989, Grzybkowska and Witczak 1990, Palmer 1990). High densities of nematodes and ceratopogonids imply that these groups may be very important in the overall energetics of the Green River system. Both should be studied more intensely. The overall dynamics of these communities is undoubtedly associated with seasonal changes in flow as well as year-to-year variability in annual discharge. This study, while describing a backwater, river site, side channel, and floodplain wetland over a short time interval, does not allow a full assessment of either annual or spatial variability. It is clear that some sort of successional colonization of various habitats occurs; for instance, floodplain wetlands are maximum in extent during highest spring-early summer flows, but their faunal development lags peak flooding. Backwaters do not exist during high flows, but as floodplains diminish with receding water levels, backwater habitats develop. Again their faunal assemblages tend to lag behind the emergence of recognized backwaters. While we documented what appears to be seasonal succession within habitat type, such changes should not be assumed the norm. Until a detailed study is undertaken for the Green River or Colorado River system with replicate habitats over at least a full year period, our observations must be considered tentative. Further, annual discharge can vary tremendously from year to year, depending upon factors such as drought cycles and their link with El Niño dynamics in the Pacific. Thus, what is seen in one year may not be representative of all years. Such factors introduce additional variables that should be considered when attempting to understand the dynamics of the benthos of the Green River.

#### LITERATURE CITED

- ADAMEK, Z., AND I. SUKOF 1992. Invertebrate communitics of former southern Moravian floodplains (Czechoslovakia) and impacts of regulation. Regulated Rivers: Research and Management 7: 181–192.
- BECKETT, D. C., C. R. BINGHAM, AND L. G. SANDERS. 1983. Benthic macroinvertebrates of selected habitats of the lower Mississippi River. Journal of Freshwater Ecology 2: 247–261.
- BERG, M. B., AND R. A. HELLENTHAL. 1991. Secondary production of Chironomidae (Diptera) in a north temperate stream. Freshwater Biology 25: 497–505.
- BOTT, T. L., AND L. A. KAPLAN. 1989. Densities of benthic protozoa and nematodes in a piedmont stream. Journal of the North American Benthological Society 8: 187–196.
- BOWEN, T. W. 1983. Production of the predaceous midge tribes Sphaeromiini and Palpomyiini (Diptera: Ceratopogonidae) in Lake Norman, North Carolina. Hydrobiologia 99: 81–87.
- BOWMAN, C. M. T. 1980. Emergence of chironomids from Rosterne Mere, England. Pages 291–295 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349.
- BRINKHURST, R. O., AND D. G. СООК. 1974. Aquatic earthworms (Annelida: Oligochaeta). Pages 143–156 *in* C. W. Hart, Jr., and S. L. H. Fuller, editors, Pollution ecology of freshwater invertebrates. Academic Press, New York.
- BRINKHURST, R. O., AND S. R. GELDER. 1991. Annelida: Oligochaeta and Branchiobdellidi. Pages 401–433 in J. H. Thorp and A. P Covich, editors, Ecology and classification of North American freshwater invertebrates. Acedemic Press Inc., San Diego, CA.
- BROWN, A. E., R. A. OLDHAM, AND A. WARLOW. 1980. Chironomid larvae and pupae in the diet of brown trout (Salmo trutta) and rainbow trout (Salmo gairdneri) in Rutland Water, Leicestershire. Pages 323–329 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- CORKUM, L. D. 1990. Intrabiome distributional patterns of lotic macroinvertebrate assemblages. Canadian Journal of Fisheries and Aquatic Sciences 47: 2147–2157.
- CRANSTON, P. S. 1982. A key to the larvae of the British Orthocladiinae (Chironomidae). Freshwater Biological Association. Scientific Publication 45.
- DAVIES, F. G., AND A. R. WALKER. 1974. The isolation of ephemeral fever virus from cattle and Culiciodes midges in Kenya. Veterinary Record 95: 63–64.
- DOUGLAS, D. J., AND D. A. MURRAY. 1980. A checklist of Chironomidae (Diptera) of the Killarney Valley catchment area Ireland. Pages 123–129 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- ELLIOT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publication 25.

- GLADDEN, J. E., AND L. A. SMOCK. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. Freshwater Biology 24: 533–545.
- GRABOWSKI, S. J., AND S. D. HIEBERT. 1959. Some aspects of trophic interactions in selected backwaters and the main channel of the Green River, Utah, 1987–1988. Bureau of Reclamation, Environmental Sciences Section, Denver, CO.
- GRZYBKOWSKA, M. 1989. Production estimates of the dominant taxa of Chironomidae (Diptera) in the modified, River Widawka, and the natural, River Grabia, central Poland. Hydrobiologia 179: 245–259.
- GRZYBKOWSKA, M., AND J. WITCZAK. 1990. Distribution and production of Chironomidae (Diptera) in the lower course of the Grabia River (central Poland). Freshwater Biology 24: 519–531.
- GRZYBKOWSKA, M., J. HEJDUK, AND P. ZIELINSKI. 1990. Seasonal dynamics and production of Chironomidae in a large lowland river upstream and downstream from a new reservoir in central Poland. Archiv für Hydrobiologie 119: 439–455.
- JONASSON, P. M., AND C. LINDEGAARD. 1979. Zoobenthos and its contribution to the metabolism of shallow lakes. Ergebnisse der Limnologie (supplement to Archiv für Hydrobiologie) 13: 162–180.
- JONASSON, P. M., AND F. THORHAUGE. 1976. Population dynamics of *Potamothrix hammoniensis* in the profundal of Lake Esrom with special reference to environmental and competitive factors. Oikos 27: 193–203.
- KOEHN, T., AND C. FRANK. 1980. Effect of thermal pollution on the chironomid fauna in an urban channel. Pages 187–194 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- KREBS, C. K. 1989. Ecological methodology. Harper Collins Publishing Co., New York.
- KWAN, W. E., AND F. O. MORRISON. 1974. A summary of published information for field and laboratory studies of biting midges, *Culicoides* species (Diptera: Ceratopogonidae). Annals of the Entomological Society of Quebec 19: 127–137.
- MASON, W. T., JR. 1968. An introduction to the identification of chironomid larvae. Federal Water Pollution Control Administration, U.S. Department of the Interior, Cincinnati, OH.
- MERRITT, R. W., AND K. W. CUMMINS, EDITORS. 1984. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque, 1A.
- MORGAN, R. P. H, R. E. JACOBSEN, S. B. WEISBERG, L. A. MCDOWELL, AND H. T. WILSON. 1991. Effects of flow alteration on benthic macroinvertebrate communities below the Brighton hydroelectric dam. Journal of Freshwater Ecology 6: 419–429.
- MUNN, M. D., AND M. A BRUSVEN. 1991. Benthic macroinvertebrate communities in nonregulated and regulated waters of the Clearwater River, Idaho, U.S.A. Regulated Rivers: Research and Management 6: 1–11.
- NALEPA, T. E, AND M. A. QUIGLEY. 1983. Abundance and biomass of the meiobenthos in nearshore Lake Michigan with comparisons to the macrobenthos. Journal of Great Lakes Research 9: 530–547.
- PALMER, M. A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek,

Virginia. Journal of the North American Benthologieal Society 9: 17–25.

- PAASIVIRTA, L., AND E. KOSKENNIEMI. 1980. The Chironomidae (Diptera) in two polyhumic reservoirs in western Finland. Pages 233–238 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- PINDER, L. C. V. 1980. Spatial distribution of Chironomidae in an English chalk stream. Pages 153–161 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- POINAR, G. O., JR. 1991. Nematoda and Nematomorpha. Pages 249–283 in J. H. Thorp and A. P. Covich, editors, Ecology and classification of North American freshwater invertebrates. Academic Press Inc., San Diego, CA.
- RADER, R. B., AND J. V. WARD. 1988. Influence of regulation on environmental conditions and the macroinvertebrate community in the upper Colorado River. Regulated Rivers: Research and Management 2: 597–618.
- ROHLF, F. J. 1992. NTSYS-pc. Numerical taxonomy and multivariate analysis system. Version 1.70. Department of Ecology and Evolution, State University of New York, Stony Brook.
- SHIOZAWA, D. K. 1985. The seasonal community structure and drift of microcrustaceans in Valley Creek, Minnesota. Canadian Journal of Zoology 64: 1655–1664.
- SHIOZAWA, D. K., AND J. R. BARNES. 1977. The microdistribution and population trends of larval *Tanypus* stellatus Coquillett and *Chironomus frommeri* Atchley and Martin (Diptera: Chironomidae) in Utah Lake, Utah. Ecology 58: 610–618.
- STATZNER, B., AND B. HIGLER. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16: 127–139.
- STRAYER, D. 1985. The benthic micrometazoans of Mirror Lake, New Hampshire. Archiv für Hydrobiologie Supplement 72: 287–426.
- SWINK, W. D., AND J. F. NOVOTNY. 1985. Invertebrate colonization rates in the tailwater of a Kentucky floodcontrol reservoir. Journal of Freshwater Ecology 3: 27–34.
- TITMUS, G., AND R. M. BADDOCK. 1980. Production and emergence of chironomids in a wet gravel pit. Pages 299–305 in D. A. Murray, editor, Chironomidae: ecology, systematics, cytology, and physiology. Proceedings of the 7th International Symposium on Chironomidae, Dublin, Ireland.
- WIEDERHOLM, T., EDITOR. 1983. Chironomidae of the Holarctic region: keys and diagnoses. Part 1, Larvae. Borgstroms Tryckeri AB, Motala.
- WINGARD, C. J., AND J. H. OLIVE. 1959. Larval Chironomidae (Diptera) of the upper Tuscarawas River of northeastern Ohio, U.S.A. Journal of Freshwater Ecology 5: 93–102.
- WINKEL, E. K., AND T. DAVIDS. 1987. Cyprinid fish and water mite reducing chironomid populations. Entomologica Scandinavica Supplementum 29: 265–267.

Received 24 January 1994 Accepted 14 November 1994